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Extended Diapause in *Coloradia pandora* Blake (Lepidoptera: Saturniidae)

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The pandora moth, *Coloradia pandora* Blake, is a periodic pest of pine forests in western United States. It is one of the largest defoliating insects in North America and an obvious food source for many forest dwellers, including man; Aldrich (1921) and Essig (1934) have documented its use by Indian tribes. Principal hosts are ponderosa pine, *Pinus ponderosa* Laws., Jeffrey pine, *P. jeffreyi* Grev. & Balf., and lodgepole pine, *P. contorta* Dougl. Larvae feed in fall, overwinter, and feed again in spring in an exposed position on pine branches. Pupae are formed in early summer in loose mineral soil at a depth of 1 to 5 inches where they overwinter.

Damaging infestations were at first recorded only for southcentral Oregon and eastcentral California. In an Oregon outbreak during 1918–26, subsequent damage to ponderosa pine stands caused by bark beetles (genus *Dendroctonus*) was far greater than the primary damage by the defoliator (Patterson, 1929). In 1937–39, an extensive outbreak occurred in northcentral Colorado, the first recorded in the Rocky Mountains, and around 4,000 lodgepole pines died as a result of the defoliation (Wygant, 1941). In 1959–66, small outbreaks occurred in Oregon, California, Colorado, Wyoming, and Utah; the Rocky Mountain outbreaks were of longest duration (Carolin and Knopf, 1968). Outbreaks have occurred only in areas of loose soils, such as those formed from pumice or decomposed granite.

After studying an outbreak in Oregon's Klamath County, Patterson (1929) stated "The generations of *Coloradia pandora* are biennial, the life cycle of the species covering a period of exactly two years. . . ." He observed that flights occurred in the even-numbered years in this particular area, although "a few stragglers departed from the cycle of the main broods and emerged in the odd years." Wygant (1941), studying an outbreak in Colorado, also found major flights in the even years but noted that a small proportion of the pupae remained in the soil through two winters, with adults emerging the following summer. Massey¹ estimated this holdover population in the same outbreak as "apparently less than 5 percent."

In recent widespread series of flare-ups, occasional deviations from the even-year flight patterns were evident. In 1961, numerous moths were collected at light traps in the Custer National Forest, Wyoming (Terrell, 1962). In 1962, both second-year larvae and adults were reported in an infestation along the Colorado-Wyoming border (U. S. Forest Service, 1963). Then, in 1964, surveys of pupal density in June and September in the Sequoia National Forest, California, revealed many unemerged pupae remaining after moth flight, indicating either a population holdover until the third year or high mortality in the pupal stage.² In 1965, an off-year flight occurred on the Winema Forest near Chemult, Oregon (Orr, 1966). On the basis of these reports and a study still in progress, Carolin and Knopf (1968) concluded that in some areas at least, a substantial part of the generation remains in the soil for two years and some individuals for three and four years.

Flexibility in the life cycle of the pandora moth is now apparent from

¹ Unpublished M. A. thesis, "The Pandora Moth (*Coloradia pandora* Blake), a Defoliator of Lodgepole Pine in Colorado." Duke Univ., Durham, N. C. 1940.

² Insect Evaluation Report, U. S. Forest Service, California Region, 1966.

the record by Aldrich (1921), which noted large larvae in the Mono Lake, California, area only in even-numbered years. It is further supported by unpublished records,³ beginning in 1957, which show major flights occurring in odd-numbered years in the Mt. Laguna area of southern California and a similar incidence in 1937 for a locality near Prescott, Arizona.⁴ These various deviations from the normal periodicity in flight years could have significant impacts on survival of the pandora moth, damage to host trees, and abundance of animals that feed on this insect.

Insight into variation in population behavior, specifically in regard to pupal diapause and moth emergence, has been obtained from a 5-year study of a sample of pandora moth pupae collected near Chemult, Oregon, on 25 August 1964. A large moth flight, occurring as expected in an even-numbered year, was just ending. Two of our entomologists, R. L. Furniss and R. G. Mitchell, were visiting the area and on inspiration dug into the soil to search for unemerged pupae. A total of 168 unemerged pupae was collected with little difficulty and turned over to the author for analysis as to viability and survival.

METHODS

At the start, obviously dead pupae were discarded and, over a period of two months, seven apparently sound pupae were dissected anteriorly to determine viability as indicated by pulsing of the aorta. The remaining pupae were placed on moist soil in sturdy cardboard boxes, overwintered in a large open shed at Portland, Oregon, and brought into a basement laboratory room early the following summer (1965) for moth emergence. The boxes were stacked on a frame in a muslin-covered cage with a sliding screened door; the soil and pupae were moistened at approximately 7-day intervals. A single, overhead bulb provided continuous subdued illumination, and laboratory temperatures ranged from 21° to 25°C. over the 2-month holding period. Three weeks after the last moth emerged, apparently dead pupae were dissected and remaining pupae were returned to the outside shed. This procedure was repeated through the summer of 1969.

RESULTS

Most of the pupae proved to be holdovers, and some emergence occurred every summer for five consecutive years. After initial dis-

³ Summary of Pandora Moth Detection Records, California Region, dated 8 March 1967, and provided by U. S. Forest Service, Division of Timber Management, San Francisco, California.

⁴ Personal communication from George R. Struble, Research Entomologist, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

TABLE 1. Emergence of *Coloradia pandora* from holdover pupae collected near Chemult, Oregon, in August 1964.

Year	Pupae in rearing	Adults emerging		Pupae dissected	
		Males	Females	Living	Dead
		<i>Number</i>			
1964	168	—	—	7	11
1965	150	19	8	0	13
1966	110	26	15	2	9
1967	58	4	9	0	0
1968	45	5	16	0	5
1969	19	2	8	1	8
Totals	168	56	56	10	46

sections in 1965, 150 apparently sound pupae remained. From this number of pupae, 112 adults were reared and 38 pupae were dissected or broken open to verify obvious or suspected mortality. One pupa remained alive after emergence ended in 1969 but was dissected.

The sex ratio of adults obtained was equal for the 5-year period, with 56 males and 56 females emerging. However, males predominated in the first two years, when emergence was heaviest; and females predominated in the next three years. The incidence of female emergence increased from around 30 percent in 1965 to around 80 percent in 1968 and 1969. Data are summarized in Table 1.

No attempt was made to mate insects in 1965, but in 1966 and 1967 some females were mated and laid fertile eggs. In 1968, male and female emergence intermeshed, and it was assumed that mating would take place without stimulation, such as exercising the males. However, no mating occurred. In 1969 only two males were available for mating; one was crippled at emergence and the other emerged when no females were available.

Oviposition from 1966 and 1967 matings appeared normal. Four gravid females in 1966 laid an average of 77 eggs, and two gravid females in 1967 laid an average of 118 eggs. Most of the eggs hatched, and larvae fed normally on pine foliage provided them. Another female in 1967 found a mate after it had laid infertile eggs, and five of 14 eggs subsequently laid proved fertile.

DISCUSSION AND CONCLUSIONS

Diapause of pandora moth pupae collected after moth flight in 1964 lasted as long as five years, with a single living pupa going into its

sixth year in diapause. Since the age of these pupae was unknown when collected, the duration of diapause could be six years or longer. Diapause under field conditions could be further extended by lack of suitable soil temperatures for physiogenesis. In studies on *Saturnia pyri* Schiffermüller, Rivnay and Sobrio (1967) found that termination of diapause and activation of physiogenesis took place within a restricted temperature range.

Some emergence of pandora moth must take place every year. And, in so-called "flight years," the adults must stem from pupae of different ages. The majority, however, are probably from pupae which have been in the soil one year, as indicated by earlier observers.

These results indicate that pupal density surveys to estimate adult populations will overestimate these populations in flight years and fail to consider off-year flights. Until more is known about the diapause components in different populations, correction factors should be determined by rearing overwintered pupae found in the surveys to estimate percent emergence for the coming summer.

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